

Plants of Western Australian granite outcrops

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Abstract

Outcropping granite rocks in Western Australia span a considerable climatic range, from the mediterranean south-west to inland desert and northern arid subtropics and tropics. At least 1320, and possibly 2000, plant taxa occur on Western Australian granite outcrops. Outcrop plant life is most diverse in the South West Botanical Province, with individual outcrops having up to 200 species, including many endemics not found in surrounding habitats. Species richness and local endemism declines with increasing aridity, to the point where Kimberley and Pilbara outcrops show little discontinuity in species from the surrounding landscape matrix. Outcrops are dominated by woody and herbaceous perennials, especially of the Myrtaceae, Orchidaceae, and Mimosaceae, and have an unusually rich diversity of annuals (Asteraceae, Styliaceae, Poaceae, Amaranthaceae *etc.*) compared with the flora as a whole. An unusual life form is found in resurrection plants capable of extreme desiccation and rehydration (*e.g.* *Borya*, *Cheilanthes*). Among woody perennials, bird pollination is frequent, and some outcrops harbour a high proportion of obligate seeder species due to the refuge from fire provided by bare rock barriers. The diversity of microhabitats and soil moisture regimes on outcrops has enabled the persistence of species beyond their main range in the face of climatic fluctuations. It has also facilitated the evolution of many endemics in the south-west. Major threatening processes facing outcrop plant communities include weed invasion, grazing by stock and feral animals, too-frequent fire, clearing, loss of shrub layer, salinity, and dieback. Conservation of these rich rare habitats needs the support of local communities.

Introduction

Western Australia is the largest Australian State, extending 2 391 km north-south and 1 621 km east-west, and occupying 2 525 500 km², or about a third of the nation. Climates range from temperate and mediterranean in the south-west to the monsoonal tropics in the extreme north, with arid conditions prevailing over much of the State from the Nullarbor Plain north through the inland deserts to the north-west Pilbara and Kimberley regions.

Most of the State is a plateau 300-600 m above sea level, with the highest point (Mt Meharry) only 1 251 m. Western Australia's numerous granite inselbergs and outcrops, consequently, are significant landscape features, even though most emerge less than 100 m above surrounding terrain.

Granite (or granitoid) rocks are mainly found on the Yilgarn and Pilbara Cratons, which together occupy about a third of the State's landmass, and along adjacent south coastal and Kimberley orogens (Myers 1997). The outcrops thus span a considerable climatic range, from the mediterranean south-west to inland desert and northern arid subtropics and tropics.

Western Australian outcrops vary in area from about

one tenth of a hectare to many hectares. While most are clearly isolated and disjunct, sometimes separated from the next outcrop by tens of kilometres, others are part of extensive inselberg systems covering several square kilometres (*e.g.* outcrop systems in Cape Le Grand, Porongurups and Cape Arid National Parks on the south coast, at Oudabunna Station near Paynes Find, and at Woodstock Station in the Pilbara). Peak Charles, 100 km north-west of Esperance, stands highest above surrounding country among the State's inselbergs, reaching 500 m from a low plain.

While the Kimberley, Pilbara and desert granites are in regions with depauperate floras not unlike those of much of tropical and arid Australia, the granite of the Yilgarn Craton underlies one of the world's regions richest in plant life, the South West Botanical Province (Marchant 1973; Hopper 1979, 1992; Beard 1980, 1981, 1990). As many as 8000 vascular plant species occur in this region, with about 75% endemism. Consequently, the botanical exploration of south-western inselbergs has been particularly rewarding, and much remains to be done.

Here, we provide an overview of current knowledge of plant life on Western Australian granite outcrops. Our aim was to compile a baseline, including a preliminary list of plants (vascular and cryptogam) collected from Western Australian outcrops, and a list of key references, to inform future research and provide a context for more specific studies. We conclude with some thoughts on the

conservation of this special component of Western Australian plant life.

Botanical Exploration

Western Australian granite outcrops have been important to aboriginal people ever since they occupied the land, but little has been documented of this long-standing relationship (Bindon 1997). Recorded European knowledge of granite outcrop plants in the State commenced with Archibald Menzies, surgeon and naturalist aboard the *HMS Discovery*, under the command of Captain George Vancouver. The *Discovery* was anchored in King George's Sound from September 28 to October 11, 1791.

Menzies made a "copious collection of ... vegetable productions, principally the genus *Banksia*, which are here very numerous" from various sites onshore in the vicinity of present-day Albany (Maiden 1909). Given the prominence of granite headlands, hills and islands at Albany, Menzies undoubtedly collected from them, but details are difficult to trace.

European botanists first named granite outcrop plants from Western Australia in 1800. The Frenchman Jacques J H de Labillardiere was naturalist on Admiral Bruny d'Entrecasteaux's expedition to Australia, which sought refuge from a storm near the modern town of Esperance over the period 9-17 December 1792. Labillardiere's specimens included a plant he named in 1800 as *Eucalyptus cornuta*, collected from the granite Observatory Island on 13 December 1792. *E. cornuta* occupies the apron and deeper soil pockets on granite outcrops throughout the Esperance area and adjacent islands, extending westwards to the Cape Naturaliste area (Fig 1).

Labillardiere named other granite outcrop plants from the expedition, including the bizarre genus *Borya* (Fig 4), a pincushion lily and resurrection plant, named in 1805 and typified by the species *B. nitida* which occurs on shallow soils on outcrops along the south coast from Albany to east of Esperance.

Robert Brown, on the expedition to circumnavigate Australia led by Matthew Flinders in the *Investigator*, anchored at King George's Sound on December 8, 1801, and collected extensively until January 5, 1802. Between January 10-18, the expedition also explored and collected near Esperance, landing at Lucky Bay (in the present-day Cape Le Grand National Park) for five days, and on islands in the Recherche Archipelago. Brown (1810) also named many granite outcrop plants, including another species of *Borya* (*B. spaherocephala*) that occurs with *B. nitida* on several south coast outcrops.

The arrival of James Drummond at the Swan River with Captain Stirling's colonising party on the *Parmelia* in 1829 heralded a major advance in knowledge of the south-west's flora, including that of granite outcrops (Erickson 1969). Drummond, a Scot and keen nurseryman with an excellent eye for new taxa, collected widely throughout the forests and present day wheatbelt, his specimens destined for subscribers in Great Britain and Europe. He was followed by many others up to modern times. Beard (1981) provides a useful historical review. The floral wealth of the south-west is such that significant numbers of new taxa

continue to be discovered and described each year (Green 1985; Hopper 1992), including granite outcrop endemics.

The ecology and biogeography of Western Australian granite outcrop plants were observed by the earliest collectors, but drew specific mention by the plant geographer Ludwig Diels (1906), who noted the "dwarflike" vegetation. Smith (1962) provided an account of the vegetation of the granite Porongurup Range, and many others have mentioned granite outcrop plants in broader vegetation surveys in the south-west (e.g. Beard 1981; Newbey & Hnatiuk 1985; Newbey *et al.* 1995; Wardell Johnson & Williams 1996; Brooker & Margules 1996).

Main (1967) gave a delightful account of the natural history of Yorkrakine Rock through an annual cycle. Marchant (in Erickson *et al.* 1973) summarised botanical features of south-western outcrops in an essay for a general readership.

Schweinfurth (1978) described the vegetation of exposed granite headlands along the south coast, while Abbott & Watson (1978) and Abbott (1980) explored these headlands and adjacent islands in greater detail, showing the flora of most islands had a depauperate subset of that found onshore, and displayed little endemism nor genetic differentiation from mainland populations.

Hopper (1981) highlighted the importance of winter-flowering woody perennials as a nectar resource used by a diversity of honeyeaters in the central wheatbelt (Fig 3). Pate & Dixon (1982) gave a comprehensive account of the biology of tuberous and cormous plants, including many found on granite.

Ornduff (1987) documented the flora of herbfields including, and centrewards from, the *Borya* zone on nine outcrops near Perth and Hyden. Burgman (1987) sampled five outcrops inland from Esperance and explored aspects of rarity in granite communities. Hopper *et al.* (1990) illustrated 29 endangered endemics of granite outcrops and highlighted conservation issues. Pignatti & Pignatti (1994) reported on herbfields from shallow seasonally wet soils on a selection of south-west outcrops. Ohlemüller (1997) documented plants in shallow soil depressions on 26 outcrops throughout the south-west and goldfields.

In parallel with these ecological investigations, genetic studies of Western Australian granite outcrop plants were pioneered by James (1965), who's penetrating work on the herb *Isotoma petraea* (Lobeliaceae) has become a classic in the literature on plant evolution (Bussell & James 1997). Studies on the population genetics of endemic granite outcrop eucalypts have also provided useful insights into the evolution of highly fragmented small populations (Moran and Hopper 1983; Sampson *et al.* 1988). The breeding systems of granite outcrop endemics have been documented for *Villarsia* (Menyanthaceae; Ornduff 1986, 1996) and *Anthocercis gracilis* (Solanaceae; Stace 1995).

Sampling Methods

Rather than laboriously search the increasing number of botanical publications that include plant taxa recorded

on Western Australian granite outcrops, we compiled the plant list from specimens housed in the Western Australian Herbarium. The database WAHERB stores full label details of 413 000 specimens of vascular plants and cryptogams collected throughout the State, and afforded an opportunity to list those taxa for which habitat details on labels included the words "granite outcrop". Initial trials indicated that searching on "granite" or "granitic" alone picked up too many taxa that occupied regions underlain by granite rock, but favoured deep soils well removed from rock outcrops.

In our list, taxa are mainly species, but infraspecific subspecies, varieties and forms, together with hybrids, are all counted. This ensures that all named plant biodiversity is included, and allows for discrepancies in assigning rank among taxonomists.

The above approach to listing plant taxa was based on an understanding that most authors involved in botanical survey of Western Australian granite outcrops have collected voucher specimens and deposited them in the Western Australian Herbarium (e.g. Ornduff 1987; Burgman 1987; Hopper 1981; Hopper *et al.* 1990; Hopper & Brown, *unpublished orchid research*; Newbey & Hnatiuk 1985; Newbey *et al.* 1995). In addition, as an independent check, the senior author has compiled field herbaria in notebooks for *ca* 150 outcrops throughout Western Australia over the past two decades. Most outcrops sampled occur in the South West Botanical Province (e.g. Fig 1) and adjacent pastoral region, while a few have been examined in the Pilbara (e.g. Fig 2) and Kimberley.

Precisely defining the boundaries of a granite outcrop is difficult, especially for mobile components of the biota (Main 1997). However, the sedentary nature of adult plants, especially perennials, affords a reliable and measurable biological indicator of the limits of the outcrop system.

In fieldwork, we have used the distribution of plants that are locally endemic to outcrops to define the extent of outcrop communities sampled. Thus, all species centrewards from the outermost individuals of granite outcrop local endemics were included as present on an outcrop. This approach ensures that all endemics are sampled, but has the effect of picking up some species from surrounding deeper soils that do not extend onto soil pockets on the outcrop itself. Other authors have restricted their sampling to such soil pockets (e.g. Houle 1990; Porembski *et al.* 1995; Ohlemuller 1997), or only to herbfields (e.g. Ornduff 1987). Experience showed that perennial vegetation fringing the base of Western Australian outcrops had to be sampled to ensure a comprehensive inventory (see below).

We followed Newbey and Hnatiuk (1985) and Newbey *et al.* (1995) in collecting on random walks stratified by microhabitat rather than within quadrats *i.e.* the *random stratified walk* technique. A comparison of the senior author's data with the quadrat-based data of Burgman (1987) for Mt Ney inland from Esperance showed that four 5m x 5m quadrats spaced at 25 m intervals on NE scree slope and sheet rock yielded 61 taxa, whereas 192 taxa were documented through random stratified walks covering cardinal compass points.

Microhabitats recognised and deliberately searched

for on random stratified walks included bare rock, cryptogamic crusts, gnammas (rock pools or weather pits, seasonal and permanent), soil-filled crevices, caves/tafoni/shade of boulders or exfoliated slabs, herbfields on shallow well-drained soil, herbfields on shallow seasonally waterlogged soil (ephemeral flush vegetation), shrublands and woodlands on deep well-drained soil, shrublands, woodlands and forests on deep seasonally waterlogged soil, permanent springs, major watercourses, and salt lakes.

Floristics

A total of 1320 Western Australian granite outcrop plant taxa were represented and labelled as such in the collections of the Western Australian Herbarium in May 1996 (Appendix 1). Of these, 1097 taxa (83.0%) were described, 94 (7.1%) were undescribed but well-delimited with manuscript names, and 129 (9.9%) were of uncertain taxonomic delimitation. Only 4 (0.3%) were hybrids, well below the proportion (4%) estimated for the whole WA flora (Hopper 1995). The list includes 11 macrofungi, 34 lichens, 46 mosses, 9 liverworts, 9 ferns, 7 fern allies, 2 cycads, 2 conifers, and 1200 angiosperms (284 monocotyledons, 916 dicotyledons).

While these statistics provide a useful baseline, it is pertinent to note that sampling of most cryptogam groups is poor. For example, we recorded only 34 lichens with vouchered granite outcrop specimens for the whole of WA, whereas Pigott & Sage (1997) list 36 lichen taxa for Yilliminning Rock alone. Macrofungi undoubtedly are orders of magnitude more diverse than presently known. The moss flora is comparatively better documented at the species level (Stoneburner *et al.* 1993; Stoneburner & Wyatt 1996), but much more collecting is needed to fill in knowledge of distribution and ecology.

Some confidence may be placed in the list of vascular plant taxa, which accounts for 1220 (92.4%) of the total of 1320. Based on our knowledge of rock outcrop floras across the State, the majority of south-western vascular plant taxa on granite outcrops are listed. However, some conspicuous omissions of taxa that are common (e.g. *Hakea petiolaris*, *Corymbia calophylla*), uncommon (e.g. *Grevillea magnifica*, *Phylloglossum drummondii* and *Isoetes drummondii*) and rare (e.g. *Drummondita hassellii* var *longifolia*, *Hibbertia bracteosa*, *Villarsia calthifolia*, *Pleurophascum occidentale*) indicate that revision upwards is required. Moreover, a comparison of the list of 187 taxa for Yilliminning Rock near Narrogin (Pigott & Sage 1997) with Appendix 1 shows that 78 Yilliminning taxa (42%) are not present in our list for the State. This discrepancy would be even more so for northern outcrops. For example, absent from the present list are the dominant spinifex hummock grasses on granite outcrops (*Triodia* spp), as well as common lemon grasses (*Cymbopogon* spp), and scattered but widespread subtropical woody shrubs and small trees such as *Terminalia canescens*. It would be no surprise to us, consequently, if the number of vascular plant taxa on Western Australian granite outcrops approached 2000 in the future.

In the present list, major vascular plant families include the Myrtaceae (162 taxa), Orchidaceae (159), Mimosaceae

(82), Asteraceae (72), Papilionaceae (66), Proteaceae (54), and Stylidiaceae (33). Genera richest in taxa on granite outcrops include *Acacia* (82 taxa), *Caladenia* (70), *Eucalyptus* (44), *Stylidium* (28), *Melaleuca* (26), *Grevillea* (25), *Drosera* (21), *Verticordia* (20), *Eremophila* (18) and *Thelymitra* (16).

Thus, woody perennial shrubs and trees of myrtles, wattles, peas and Proteaceae are taxon-rich on WA granite outcrops, reflecting trends in the flora as a whole (Green 1985; Hopper *et al.* 1996). However, the granite woody perennials are depauperate in Epacridaceae, which is rich in other habitats. The granite outcrop flora is clearly divergent from the flora at large in the unusually high taxon richness of groups such as the tuberous perennial terrestrials (orchids, sundews, lilies), and herbaceous, often annual, daisies and triggerplants.

Systematic sampling of shallow-soil herbfields on south-western outcrops by Ornduff (1987) and Ohlemüller (1997) yields a useful comparison with our data on herbaceous families. Ornduff recorded 160 taxa belonging to 37 families (he didn't sample Orchidaceae for conservation reasons), of which the largest were Asteraceae, Poaceae, Liliaceae *sens. lat.*, and Stylidiaceae. Ohlemüller recorded 134 species from 42 families, with the largest being Asteraceae, Orchidaceae, Poaceae, Apiaceae, Stylidiaceae and Centrolepidaceae.

Major herbaceous families in our list are Orchidaceae (Fig 5), Asteraceae, Stylidiaceae, Anthericaceae (or Liliaceae *sens. lat.*), Poaceae, Droseraceae, Cyperaceae, Goodeniaceae, Amaranthaceae and Centrolepidaceae. The Amaranthaceae is a family richest in the north of Western Australia, so it is not surprising that Ornduff (1987) and Ohlemüller (1997) found it to be depauperate in their south-west study areas. Orchidaceae undoubtedly emerges as the most taxon-rich herbaceous family in our list because two of us (SH and AB) have made a detailed and prolonged study of granite outcrop orchids, and found that repeat surveys over different seasons and years are needed to develop comprehensive orchid inventories for individual rocks. Other differences between our ranking and those of Ornduff (1987) and Ohlemüller (1997) are minor. This general concordance suggests that major trends and statistics for the vascular plants in Appendix 1 are accurate, at least for south-west outcrops.

Plants of Special Interest

Granite outcrop habitats have elicited remarkable parallel evolution in many plants and animals (Porembski *et al.* 1997; Wyatt 1997; Mares 1997). The combination of high solar radiation, rapid runoff of rainfall, and shallow soils on a rocky substrate provide microhabitats of accentuated seasonal and diurnal stresses. Conditions may vary over a few metres from cool permanently moist shaded caves with water seepage to drought-afflicted shallow soils and rock surfaces fully exposed to all the elements.

Few organisms can tolerate the harshest of these rock-surface habitats, which tend to be occupied by cryptogamic crusts of cosmopolitan cyanobacteria, lichens and mosses such as *Grimmia laevigata*. Western Australian outcrops conform to this trend. However, on

south-west outcrops experiencing high rainfall, moss cushions become prominent, with the luxuriant brown carpets of *Breutelia affinis* and the verdant green *Campylopus bicolor* and *C. australis* noteworthy.

Coping with seasonal or unpredictable drought is, undoubtedly, the most significant survival strategy faced by granite outcrop plants. Among Western Australian herbaceous perennials on outcrops, pincushion lilies (*Borya* spp, Boryaceae) are abundant and remarkable in their capacity as resurrection plants (Gaff 1981) to withstand desiccation to less than 5% of normal leaf moisture content, turning orange in the process, and rehydrating to normal green leaves within a day of rainfall (Fig 4). There are at least six species of *Borya* in the South West Botanical Province (*B. sphaerocephala* is a variable taxon awaiting detailed study and possible subdivision). These plants do not extend to the Pilbara outcrops. Other resurrection plants commonly seen on WA granites include the rock ferns *Cheilanthes* spp and *Pleurosorus rutifolius*.

Persisting underground as a tuber during drought is a common strategy among Western Australian granite outcrop herbs in the south-west and adjacent pastoral regions, especially lilioids (e.g. *Wurmbea* spp, Colchicaceae), orchids (*Caladenia*, *Thelymitra*, *Pterostylis*, *Diuris*, *Prasophyllum*) and sundews (*Drosera*), as well as the unusual fern ally *Phylloglossum* (Pate & Dixon 1982). On northern outcrops, tuberous Cyperaceae tend to occupy this niche.

Succulence is not prominent in the Western Australian granite outcrop perennial floras, but has evolved in a few taxonomically-unrelated species e.g. *Spiculaea ciliata* (Orchidaceae; Fig 5), *Carpobrotus* spp (Aizoaceae). Some perennial shrubs of south coast granites have unusually thick leaves (e.g. *Hakea clavata*, Proteaceae; *Anthocercis viscosa*, Solanaceae), and at least one has tuberous roots (*Calothamnus tuberosus*, Myrtaceae). Sclerophyllous leaves characterise the vast majority of woody perennials found on granite outcrops, as well as in the Western Australian flora at large.

The graminoid habit has evolved in several unrelated groups in the south-west, with common perennials forming tussocks including diverse Cyperaceae (especially *Lepidosperma* spp), blind grass (*Stypandra* spp, Phormiaceae), the sedge-like grass *Spartochloa scirpoidea* (Poaceae) and lemon grass *Cymbopogon* spp (Poaceae). Desert, Pilbara and Kimberley outcrops are dominated by uniquely Australian hummock grasses with inrolled pungent leaves (*Triodia* spp, Poaceae).

Drought avoidance through an annual life history is a major feature of Western Australian granite herbs in families such as the Asteraceae, Stylidiaceae, Poaceae, Goodeniaceae, Amaranthaceae and Centrolepidaceae. Most of these annuals have relatively small inconspicuous flowers suggestive of inbreeding (Ornduff 1987), but some are brightly coloured and abundant. Most outcrops in southern Western Australia are bedecked with colourful swards of annual triggerplants (*Stylidium*, Stylidiaceae) and everlastings (e.g. *Rhodanthe*, *Waitzia*, Asteraceae) that enliven the herbfields. Succulence is a feature of some annuals, especially those that occupy the dry spectrum of shallow soils (e.g. *Calandrinia* spp, Portulacaceae; *Crassula* spp, Crassulaceae).



1. Coastal granite outcrops east of Albany on Two Peoples Bay Nature Reserve, with *Eucalyptus cornuta* (pale canopy), described in 1800 by French scientific explorer Labillardiere. Photograph by SD Hopper.



2. Granite sheet, boulders and distant inselbergs in the arid Pilbara, Spear Hill, south-west of Marble Bar. Photograph by SD Hopper.



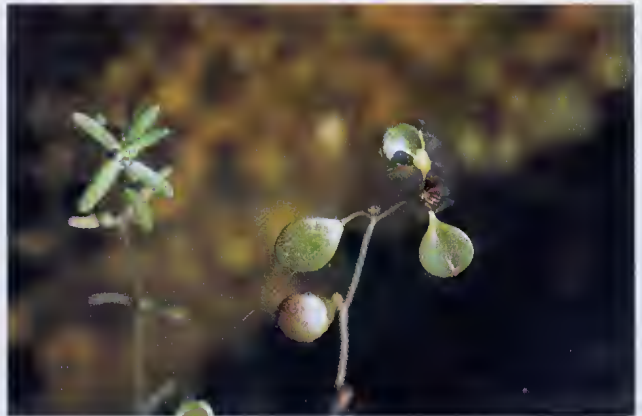
3. Bird-pollinated plants are a feature of south-west Australian granite outcrops - New Holland Honeyeater on *Eucalyptus caesia*, Boyagin Rock, north-west of Pingelly. Photograph by SD Hopper.



4. The resurrection plant, pincushion lily *Borya constricta*, with leaves 1 cm long desiccated (orange) but rehydrating (green) following rain at the end of summer drought, Chiddarcooping Rock, north-east of Merredin. Photograph by SD Hopper.



5. Terrestrial orchids are the second most species-rich plant family on Western Australian granite outcrops. Here, flowers of the elbow orchid (*Spiculaea ciliata*) 1 cm long splay from the succulent stem that feeds them in early summer, and a male thynnid wasp attempts to copulate with the flower's sexual decoy, an insectiform hinged labellum, Boulder Rock, Brookton Highway. Photograph by BA & AG Wells.



6. Arguably the rarest Western Australian granite outcrop plant, the annual aquatic millfoil *Myriophyllum lapidicola* in full flower (with round floating leaves), and known from just two gnammas (rock pools), alongside the invasive aquatic South African weed, *Crassula natans* var *minus*. Photograph by SD Hopper.

Annuals are also found commonly in seasonally waterlogged shallow soils or ephemeral flush communities (Pignatti & Pignatti 1994). These annuals include species of Centrolepidaceae (*Centrolepis* and *Aphelia*), Apiaceae (*Hydrocotyle*), Juncaginaceae (*Triglochin*), Cyperaceae (*Schoenus*, *Isolepis*, *Cyperus*), Asteraceae (*Quinetia*, *Millotia*, *Rutidosis*, *Siloxerus*, *Toxanthes*, *Hyalosperma*, *Podotheca* etc.) and Styliidiaceae (*Styloidium*, *Levenhookia*).

Deeper soils enable survivorship of woody perennials, of which the largest on Western Australian outcrops include eucalypts (*Eucalyptus* and *Corymbia*, Myrtaceae), wattles (*Acacia*, Mimosaceae), she-oaks (*Allocasuarina*, Casuarinaceae), and rock figs (*Ficus*, Moraceae). A noteworthy feature of the woody perennials is the high proportion of bird-pollinated species (Hopper 1981; Fig 3) in families such as Myrtaceae (e.g. *Eucalyptus*, *Calothamnus*, *Melaleuca*, *Verticordia*), Proteaceae (*Grevillea*, *Hakea*, *Banksia*), Myoporaceae (*Eremophila*), Papilionaceae (*Kennedy*, *Crotolaria*), Viscaceae (*Amyenia*, *Lysiana*) and Sterculiaceae (*Brachychiton*). Also, south-western outcrops have an unusually high number of woody perennials that are obligate seeders - plants that are killed by fire and recruit only from seed. For example, 77% of the perennials in a granite community at Chiddarcooping Nature Reserve north-east of Merredin were obligate seeders (Hopper *et al.*, unpubl.).

Gnammas on Western Australian outcrops have a unique flora comprising annual species of quillworts (*Isoetes*, Isoetaceae), mudmats (*Glossostigma*, Scrophulariaceae), millfoils (*Myriophyllum*, Haloragaceae; Fig 6) and others, including the introduced South African annual *Crassula natans* (Crassulaceae).

Weeds

Ornduff (1987) and Ohlemüller (1997) found that introduced weed species, mainly annuals, comprised 23.7% and 17.0% of the granite herbfield floras sampled respectively. These figures are high compared with the ca 9% that weeds represent of the WA flora as a whole (Green 1985; Keighery 1995). They are even more significant when considered with granite outcrop herbfield floras elsewhere on earth, which have far fewer invasive weeds (Porembski *et al.* 1997; Wyatt 1997).

Weed growth is most pronounced in full sun on outcrops, especially where soil has been disturbed and enriched by rabbit dung or agricultural activity. In these situations, annual grasses such as *Briza maxima*, *Avena fatua* and *Elrharta longifolia* often dominate and replace native annuals throughout much of the south-west. Weeds are rare only where a dense shrub layer or low forest of native woody perennials persist. It is clear that a persistent seed rain of weeds occurs over vast regions of the south-west, as weeds appear in open areas on outcrops where little or no disturbance is evident and native plants dominate.

Hopper (1997) has attributed the high invasibility of disturbed Western Australian plant communities to the absence of major glacial soil stripping as an evolutionary force acting on the flora. Native species are unable to compete against weeds from habitats where soil disturbance is a regular perturbation. Further

experimental study of weeds in granite herbfields could test this hypothesis, and assist attempts at restoration of invaded outcrops.

Biogeography and Endemism

Western Australian granite outcrops display plant biogeographic patterns that mirror that of the whole flora (Hopper 1979, 1992; Hopper *et al.* 1996); species-richness and endemism are pronounced in the transitional rainfall zone (wheatbelt) of the south-west, and attenuate as rainfall decreases through the pastoral country to the deserts, Pilbara and Kimberley. For example, the total number of vascular plant taxa recorded by the senior author and colleagues on a sample of rocks ranged from 142 (Point Matthew, near Augusta) and 201 (Mt Frankland) in the highest rainfall forests, 192 (Mt Ney) and 187 (Yilliminning Rock near Narrogin; Pigott and Sage 1997) in the transitional rainfall zone, to 85 (Daggar Hills, near Yalgoo) in the pastoral zone, and 90 (Moolyella Rocks, east of Marble Bar) and 80 (Spear Hill, west of Marble Bar; Fig 2) in the arid Pilbara.

There are no vascular species shared between northern (Kimberley, Pilbara) outcrops and those in the south-west. Moreover, the northern outcrop floras are virtually identical with that from the matrix of surrounding terrain, save for outcrop specialists like rock figs and rock ferns. Walters & Wyatt (1982) similarly recorded low endemism and little discontinuity between vascular plants on granite outcrops and adjacent landforms of the arid Central Mineral Region of Texas.

In contrast, south-western and adjacent pastoral zone rocks have higher levels of local endemism, especially in the high rainfall forest region where the outcrops present the most striking difference in habitat to the surrounding vegetation matrix (e.g. Wardell Johnson & Williams 1996; Brooker & Margules 1996).

Biogeographical relationships of outcrop floras across the south-west are under ongoing study by the senior author. As a precursor, Hopper & Brown (*unpublished*) documented the distribution of 126 orchid taxa on 41 outcrops ranging from the highest rainfall forests through the transitional zone wheatbelt to the arid zone. Each rock outcrop was treated as a site in a classification of the orchid data.

The study highlighted a number of significant trends. A primary division occurred between the 15 rocks found in the forested High Rainfall Zone (>800 mm *p.a.*) and the rest ranging from the Transitional Rainfall Zone of the wheatbelt into the Arid Zone. Subsequent divisions established as much difference among forest rocks as among the wheatbelt/arid rocks, even though the forest rocks were confined to a much smaller area. Moreover, remarkably, closely adjacent rocks were widely separated in the classification, indicating significant differences in their orchids (e.g. 10.3 km Rock and 10.9 km Rock of Ornduff's (1987), separated by just 600 m of jarrah forest on Albany Highway). Conversely, rocks separated geographically often had similar orchid floras (e.g. Boyagin Rock and Pingaring Rock on the western and eastern sides of the south-central wheatbelt respectively).

These patterns suggest significant barriers to orchid

Table 1

Lists of Western Australian orchid taxa that occur on granite outcrops.

All taxa		
<i>Caladenia attingens</i> subsp <i>attingens</i> ms	<i>Caladenia voigtii</i> ms	<i>Pterostylis aspera</i>
<i>Caladenia attingens</i> subsp <i>gracillima</i> ms	<i>Corybas recurvus</i>	<i>Pterostylis barbata</i>
<i>Caladenia brevisura</i> ms	<i>Cyanicula amplexans</i> ms	<i>Pterostylis elegantissima</i>
<i>Caladenia brownii</i> ms	<i>Cyanicula ashbyae</i> ms	<i>Pterostylis hamiltonii</i>
<i>Caladenia caesarea</i> subsp <i>maritima</i> ms	<i>Cyanicula caerulea</i> subsp <i>apertala</i> ms	<i>Pterostylis mutica</i>
<i>Caladenia caesarea</i> subsp <i>transiens</i> ms	<i>Cyanicula deformis</i> ms	<i>Pterostylis recurva</i>
<i>Caladenia citrina</i> ms	<i>Cyanicula fragrans</i> ms	<i>Pterostylis roensis</i>
<i>Caladenia denticulata</i>	<i>Cyanicula genuata</i> ms	<i>Pterostylis sanguinea</i>
<i>Caladenia dimidia</i> ms	<i>Cyanicula sericea</i> ms	<i>Pterostylis sargentii</i>
<i>Caladenia discoidea</i>	<i>Cyrtostylis huegelii</i>	<i>Pterostylis scabra</i>
<i>Caladenia douthchiae</i>	<i>Cyrtostylis robusta</i>	<i>Pterostylis vittata</i>
<i>Caladenia exstans</i> ms	<i>Diuris aff longifolia</i>	<i>Pyrorchis nigricans</i>
<i>Caladenia falcata</i>	<i>Diuris brunalis</i>	<i>Spiculaea ciliata</i>
<i>Caladenia filifera</i>	<i>Diuris conspicillata</i>	<i>Thelymitra aff holmsii</i>
<i>Caladenia flaccida</i> subsp <i>flaccida</i> ms	<i>Diuris laevis</i>	<i>Thelymitra aff longifolia</i>
<i>Caladenia flaccida</i> subsp <i>pulchra</i> ms	<i>Diuris laxiflora</i>	<i>Thelymitra aff nuda</i>
<i>Caladenia flava</i> subsp <i>flava</i> ms	<i>Diuris longifolia</i>	<i>Thelymitra aff pauciflora</i>
<i>Caladenia flava</i> subsp <i>maculata</i> ms	<i>Diuris maculata</i>	<i>Thelymitra antennifera</i>
<i>Caladenia flava</i> subsp <i>sylvestris</i> ms	<i>Diuris picta</i>	<i>Thelymitra benthamiana</i>
<i>Caladenia footeana</i> ms	<i>Diuris pulchella</i>	<i>Thelymitra crinita</i>
<i>Caladenia granitora</i> ms	<i>Diuris recurva</i>	<i>Thelymitra cucullata</i>
<i>Caladenia lieberleana</i> ms	<i>Diuris setacea</i>	<i>Thelymitra aff dedmaniarum</i>
<i>Caladenia hirta</i> subsp <i>rosea</i> ms	<i>Drakonorchis barbarossa</i> ms	<i>Thelymitra flexuosa</i>
<i>Caladenia hoffmanii</i> subsp <i>graniticola</i> ms	<i>Drakonorchis drakeoides</i> ms	<i>Thelymitra macrophylla</i>
<i>Caladenia incensa</i> ms	<i>Drakonorchis mesocera</i> ms	<i>Thelymitra spiralis</i>
<i>Caladenia incrassata</i> ms	<i>Elythranthera brunonis</i>	
<i>Caladenia infundibularis</i>	<i>Elythranthera emarginata</i>	Taxa that predominantly occur on granite outcrops
<i>Caladenia integra</i>	<i>Eriochilus dilatatus</i> subsp <i>dilatatus</i> ms	<i>Caladenia caesarea</i> subsp <i>maritima</i> ms
<i>Caladenia latifolia</i>	<i>Eriochilus dilatatus</i> subsp <i>multiflorus</i> ms	<i>Caladenia exstans</i> ms
<i>Caladenia lobata</i>	<i>Eriochilus dilatatus</i> subsp <i>undulatus</i> ms	<i>Caladenia granitora</i> ms
<i>Caladenia longicauda</i> subsp <i>clivicola</i> ms	<i>Eriochilus helonomos</i> ms	<i>Caladenia hoffmanii</i> subsp <i>graniticola</i> ms
<i>Caladenia longicauda</i> subsp <i>eminens</i> ms	<i>Eriochilus pulchellus</i> ms	<i>Caladenia integra</i>
<i>Caladenia longicauda</i> subsp <i>longicauda</i> ms	<i>Eriochilus scaber</i>	<i>Caladenia longicauda</i> subsp <i>clivicola</i> ms
<i>Caladenia longicauda</i> subsp <i>rigidula</i> ms	<i>Genoplesium nigricans</i>	<i>Caladenia longicauda</i> subsp <i>rigidula</i> ms
<i>Caladenia longiclavata</i>	<i>Leptoceras menziesii</i>	<i>Caladenia multiclavia</i>
<i>Caladenia macrostylis</i>	<i>Lyperanthus serratus</i>	<i>Caladenia nivalis</i>
<i>Caladenia marginata</i>	<i>Microtis aff parviflora</i>	<i>Caladenia remota</i> subsp <i>remota</i> ms
<i>Caladenia microchila</i> ms	<i>Microtis atrata</i>	<i>Cyanicula ashbyae</i> ms
<i>Caladenia multiclavia</i>	<i>Microtis brownii</i>	<i>Cyanicula fragrans</i> ms
<i>Caladenia nivalis</i> ms	<i>Microtis eremaea</i>	<i>Diuris conspicillata</i>
<i>Caladenia pachychila</i> ms	<i>Microtis graniticola</i>	<i>Diuris picta</i>
<i>Caladenia pholcoidea</i> ms	<i>Microtis media</i> subsp <i>eremicola</i>	<i>Diuris pulchella</i>
<i>Caladenia polychroma</i> ms	<i>Microtis media</i> subsp <i>media</i>	<i>Eriochilus pulchellus</i> ms
<i>Caladenia radialis</i>	<i>Monadenia bracteata</i>	<i>Microtis eremaea</i>
<i>Caladenia reptans</i> subsp <i>impensa</i> ms	<i>Paracaleana nigrata</i>	<i>Microtis graniticola</i>
<i>Caladenia reptans</i> subsp <i>reptans</i> ms	<i>Paracaleana triens</i> ms	<i>Microtis media</i> subsp <i>eremicola</i>
<i>Caladenia rhomboidiformis</i>	<i>Prasophyllum aff parvifolium</i>	<i>Spiculaea ciliata</i>
<i>Caladenia roei</i>	<i>Prasophyllum brownii</i>	<i>Thelymitra aff nuda</i>
<i>Caladenia saccharata</i>	<i>Prasophyllum cucullatum</i>	<i>Thelymitra aff dedmaniarum</i>
<i>Caladenia serotina</i> ms	<i>Prasophyllum elatum</i>	
<i>Caladenia sigmoidea</i>	<i>Prasophyllum fimbria</i>	Declared Rare orchid taxa of granite outcrops
<i>Caladenia splendens</i> ms	<i>Prasophyllum gibbosum</i>	<i>Caladenia caesarea</i> subsp <i>maritima</i> ms
<i>Caladenia hiemalis</i> ms	<i>Prasophyllum gracile</i>	<i>Caladenia exstans</i> ms
<i>Caladenia horistes</i> ms	<i>Prasophyllum parvifolium</i>	<i>Caladenia hoffmanii</i> subsp <i>graniticola</i> ms
<i>Caladenia pendens</i> subsp <i>pendens</i> ms	<i>Prasophyllum ringens</i>	<i>Caladenia voigtii</i> ms
<i>Caladenia remota</i> subsp <i>remota</i> ms	<i>Pterostylis aff nana</i>	<i>Thelymitra aff dedmaniarum</i>
<i>Caladenia pendens</i> subsp <i>talbotii</i> ms	<i>Pterostylis aff rufa</i>	
	<i>Pterostylis allantoidea</i>	

dispersal, particularly between forest rocks, and high levels of local extinction and stochastic events underlying the presence of orchids on individual rocks in the south-west and adjacent arid zone. There have been dynamic climatic fluctuations across the south-west for several million years as Australia drifted northwards and arid conditions overtook much of central Australia (Hopper

1979; Hopper *et al.* 1996). The diversity of microhabitats on granite outcrops provided refuge for plants adapted to both dry or wet conditions as the surrounding matrix waxed and waned climatically (Marchant 1973; Main 1997). Survivorship in small populations on granite refuges undoubtedly was a matter of chance in the face of such repeated climatic turmoil.

Interestingly, the above conditions of small disjunct outcrop populations undergoing recurrent stresses is predicted as ideal for genetic divergence and speciation (Grant 1981). Is this prediction borne out by studies of Western Australian outcrop plants? Table 1 provides a recently updated list of 141 orchid taxa recorded from Western Australian granite outcrops. Of these, 22 (16%) are more or less endemic. The endemics have geographical ranges from widespread on outcrops throughout the south-west (e.g. *Spiculaea ciliata*; Fig 5) to highly restricted to a few adjacent outcrops less than 10 km apart (e.g. *Caladenia caesarea* subsp *maritima*, *Thelymitra* aff *dedmaniarum*).

In terms of evolutionary origins, these endemics display at least three patterns (Hopper and Brown, unpublished);

- relictual, with no obvious close relatives and therefore likely to have been on granites for a long period of time (e.g. *Spiculaea ciliata*, a monotypic genus);
- derived by speciation from allopatric congeners of habitats other than granite (e.g. *C. granitora*, from coastal granites east of Albany, sister species to *C. infundibularis* of western high rainfall forests and coastal heaths; *C. hoffmanii* subsp *graniticola*, of east central wheatbelt outcrops, sister to *C. hoffmanii* subsp *hoffmanii* of lateritic loams well to the north-west in the Northampton region); and
- derived by speciation from allopatric congeners of other granite outcrops (e.g. *C. exstans*, from outcrops east of Esperance, sister to *C. integra* of western wheatbelt outcrops).

Thus, the orchid data do indeed support the hypothesis that conditions on south-west granite outcrops have facilitated genetic divergence and speciation. Genetic studies of a few other granite taxa lend further support, e.g. the herb *Isotoma petraea* (Bussell & James 1997), and eucalypts endemic to granite (Hopper & Burgman 1983; Sampson *et al.* 1988). Clearly, more work along these lines is needed.

There is a large number of granite endemics in south-western Australia, especially among the perennials that dominate the woody vegetation and herbfields. We have already shown that 16% of orchids on outcrops are endemic. For eucalypts, around 24% are endemic (Hopper, unpublished). The level of endemism for the whole granite outcrop flora is difficult to determine without more penetrating research, but there is no doubt that south-western Australia has higher levels than any other system documented (e.g. Walters & Wyatt 1982; Poremski *et al.* 1995, 1997).

The refugial opportunities offered by south-west granite outcrops are also evident in species that have highly disjunct outliers well removed from the main geographical distribution. These include populations on wet outcrop sites in much lower rainfall areas than the main species' stand (e.g. the Jilakin Rock stand of jarrah *Eucalyptus marginata*, the Twine Rock stand of *E. wandoo*, and the Kuendar stand of *E. rudis*). Conversely, arid-adapted species penetrate high rainfall areas on dry north-facing slopes of granites (e.g. populations of *Eucalyptus drummondii* west of Margaret River).

Conservation

Granite outcrops occupy a very small proportion of most Western Australian landscapes in which they occur. Especially in the south-west, the outcrop plant communities are, therefore, by definition, rare, and likely to contain rare species.

Hopper *et al.* (1990) found that endangered granite outcrop plants numbered 29 (12.2%) of the 238 plants declared in 1989 as Rare Flora under the Wildlife Conservation Act. These endangered plants ranged from large mallees (e.g. *Eucalyptus crucis* subsp *crucis*) and small trees (*Acacia denticulosa*, *Banksia verticillata*), through compact shrubs (e.g. *Drummondita hasselii* var *longifolia*, *Verticordia staminosa*) and climbers (*Kennedia beckxiana*, *K. macrophylla*) to diminutive herbs (*Tribonanthes purpurea*) and annual aquatics (*Myriophyllum petraeum*). While some endangered taxa have several populations spread across a number of disjunct outcrops, some are confined to very few localities (e.g. *Myriophyllum lapidicola*, known from just two gnammas). Accidental destruction of such populations could be catastrophic. Conservation in the wild in such cases needs to be backed up by off-site activities such as germplasm storage and artificial propagation (underway at Kings Park and Botanic Garden for *M. lapidicola* and other critically endangered granite endemics; Dixon 1994).

Apart from endangered species, the diverse communities on south-western granite outcrops are noteworthy in the rapidity with which they change within and between rocks. They are complex, ever-changing, and rare in their own right.

While many granite outcrops have been spared direct clearing due to their unsuitability for agriculture, and some are included within conservation reserves, most face threatening processes that need management if the native biota is to persist. Such processes include replacement or damage by invasive weeds, feral animals, grazing, inappropriate fire regimes, clearing, loss of shrub layer, salinity and dieback disease. We have briefly addressed the issue of weeds above, and highlighted the importance of maintaining undisturbed soil and dense shrub layers to control weeds effectively. Such restoration activities require an ongoing presence and commitment to a given outcrop. Local communities are vital in this context.

Western Australians are fortunate in being custodians of a unique and diverse suite of granite outcrop plants. We hope that this brief review will stimulate others to study and conserve what is a remarkable heritage.

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Appendix 1

Alphabetical list of Western Australian plants (vascular and cryptogams combined) represented by specimens in the Western Australian Herbarium and for which habitat descriptions on labels included the words "granite outcrop".

List is current to 28 May 1996, from the WAHERB database of 413 000 specimens collected from all habitats throughout W A. Nomenclature follows Green (1985) and subsequent amendments included in the Western Australian Herbarium's WACENSUS database. Taxa are listed alphabetically by generic, specific and infraspecific names, with entry concluded by family name. Numbers are those assigned to vascular plant families as in Green (1985). Taxa whose family names are preceded by a letter rather than a number are cryptogams as follows: B - moss (bryophyte); H - liverwort (hepatic); L - lichen; F - macrofungus. Uncertainty as to taxonomic delimitation is given by *aff*, *sp*, *?*, "unsorted", *sens. lat.*, or phrase name (e.g. *Form 'n'*, or "*walyahmoningensis*"). Well-delimited but unpublished taxa are identified by *ms* (for manuscript name). Full authorship of all names, published and unpublished, is given in Green (1985) and subsequent amendments included in WACENSUS.

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|---|---|
| <i>Acacia aciphylla</i> 163 Mimosaceae | <i>Acacia jennerae</i> 163 Mimosaceae |
| <i>Acacia acuaria</i> 163 Mimosaceae | <i>Acacia jiberdingensis</i> 163 Mimosaceae |
| <i>Acacia acuminata</i> subsp <i>acuminata</i> ms 163 Mimosaceae | <i>Acacia lasiocalyx</i> 163 Mimosaceae |
| <i>Acacia aculata</i> 163 Mimosaceae | <i>Acacia leptopetala</i> 163 Mimosaceae |
| <i>Acacia aff cyperophylla</i> 163 Mimosaceae | <i>Acacia leptostachya</i> 163 Mimosaceae |
| <i>Acacia aff rhodophloia</i> 163 Mimosaceae | <i>Acacia ligulata</i> 163 Mimosaceae |
| <i>Acacia andrewsii</i> 163 Mimosaceae | <i>Acacia linochloa</i> 163 Mimosaceae |
| <i>Acacia aneura</i> var <i>aneura</i> 163 Mimosaceae | <i>Acacia littorea</i> 163 Mimosaceae |
| <i>Acacia aphylla</i> 163 Mimosaceae | <i>Acacia lysiphloia</i> 163 Mimosaceae |
| <i>Acacia applanata</i> 163 Mimosaceae | <i>Acacia merrinthophora</i> 163 Mimosaceae |
| <i>Acacia assimilis</i> subsp <i>assimilis</i> 163 Mimosaceae | <i>Acacia merrallii</i> 163 Mimosaceae |
| <i>Acacia ayersiana</i> var <i>latifolia</i> 163 Mimosaceae | <i>Acacia microbotrya</i> 163 Mimosaceae |
| <i>Acacia browniana</i> var <i>browniana</i> (typical variant) 163 Mimosaceae | <i>Acacia monticola</i> 163 Mimosaceae |
| <i>Acacia browniana</i> var <i>obscura</i> 163 Mimosaceae | <i>Acacia multisiliqua</i> 163 Mimosaceae |
| <i>Acacia cochlearis</i> 163 Mimosaceae | <i>Acacia myrtifolia</i> 163 Mimosaceae |
| <i>Acacia conniana</i> 163 Mimosaceae | <i>Acacia olgana</i> 163 Mimosaceae |
| <i>Acacia constableri</i> 163 Mimosaceae | <i>Acacia praxii</i> 163 Mimosaceae |
| <i>Acacia coolgardiensis</i> subsp <i>coolgardiensis</i> 163 Mimosaceae | <i>Acacia pravifolia</i> 163 Mimosaceae |
| <i>Acacia coolgardiensis</i> subsp <i>effusa</i> (Pedunculate variant) 163 Mimosaceae | <i>Acacia pulchella</i> subsp <i>pulchella</i> 163 Mimosaceae |
| <i>Acacia costimiana</i> 163 Mimosaceae | <i>Acacia pulchella</i> var <i>goadbyi</i> 163 Mimosaceae |
| <i>Acacia cowaniana</i> 163 Mimosaceae | <i>Acacia puncticulata</i> ms 163 Mimosaceae |
| <i>Acacia cracentis</i> ms 163 Mimosaceae | <i>Acacia ramulosa</i> 163 Mimosaceae |
| <i>Acacia crenulata</i> ms 163 Mimosaceae | <i>Acacia redolens</i> 163 Mimosaceae |
| <i>Acacia cuneifolia</i> ms 163 Mimosaceae | <i>Acacia restiacea</i> 163 Mimosaceae |
| <i>Acacia cyclops</i> 163 Mimosaceae | <i>Acacia rigens</i> 163 Mimosaceae |
| <i>Acacia denticulosa</i> 163 Mimosaceae | <i>Acacia saligna</i> 163 Mimosaceae |
| <i>Acacia drummondii</i> subsp <i>elegans</i> Porongurup variant (RJ Cumms ms) 163 Mimosaceae | <i>Acacia scleroclada</i> 163 Mimosaceae |
| <i>Acacia ephedroides</i> 163 Mimosaceae | <i>Acacia sessilisipica</i> 163 Mimosaceae |
| <i>Acacia ericifolia</i> 163 Mimosaceae | <i>Acacia sp</i> 163 Mimosaceae |
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